

## Uncus shaped akin to elephant tusks defines a new genus for two very different-in-appearance Neotropical skippers (Hesperiidae: Pyrginae)

NICK V. GRISHIN

Howard Hughes Medical Institute and Departments of Biophysics and Biochemistry, University of Texas Southwestern Medical Center, 5323 Harry Hines Blvd, Dallas, TX, USA 75390-9050  
[grishin@chop.swmed.edu](mailto:grishin@chop.swmed.edu)

**Abstract.** Analyses of male genitalia, other aspects of adult, larval and pupal morphology, and DNA COI barcode sequences suggest that *Potamanaxas unifasciata* (C. Felder & R. Felder, 1867) does not belong to *Potamanaxas* Lindsey, 1925 and not even to the Erynnini tribe, but instead is more closely related to *Milanion* Godman & Salvin, 1895 and *Atarnes* Godman & Salvin, 1897, (Achlyodini). Unexpected and striking similarities are revealed in the male genitalia of *P. unifasciata* and *Atarnes hierax* (Hopffer, 1874). Their genitalia are so similar and distinct from the others that one might casually mistake them for the same species. Capturing this uniqueness, a **new genus** *Eburuncus* is erected to include: *E. unifasciata*, **new combination** (type species) and *E. hierax*, **new combination**.

**Key words:** phylogenetic classification, monophyletic taxa, immature stages, DNA barcodes, *Atarnes sallei*, Central America, Peru.

### INTRODUCTION

Comprehensive work by Evans (e.g. Evans, 1937; 1952; 1953) still remains the primary source of information about Hesperiidae worldwide. Evans' vision as an evolutionary biologist has added to this work's influence, and the backbone of his taxonomic arrangements reflected in identification keys has stood the test of time. In particular, the order in which the species are arranged in the keys frequently approximates our present understanding of their phylogeny. Recent revolutionary studies that shaped our views of Hesperiidae phylogeny re-aligned some of the Evans groups and introduced a molecular basis for higher classification (Warren *et al.*, 2008; Warren *et al.*, 2009). However, a more detailed second look at specific taxa reveals and rectifies numerous classification mistakes at the genus level, as masterfully done by Burns in a series of papers (e.g.

1982-1999). Most of Burns' work derives from careful analysis of genitalia, recently assisted by morphology of immature stages and molecular evidence (e.g. Burns & Janzen, 2005; Burns *et al.*, 2009; 2010). Bit by bit, the classification of Hesperiidae is being adjusted to reflect their phylogeny.

Another interesting case, which caused a long-lasting confusion with regard to classification, is discussed here. A curious statement can be found in Evans (1953: 138) about the genus *Potamanaxas*: "Superficially a compact genus: structurally *unifasciata* is abnormal in respect of the secondary sexual characters." To contrast it with all other 11 species of the genus, *P. unifasciata* is placed first in Evans' *Potamanaxas* key, with all these "abnormal" characters listed, and he states: "gnathos absent." A few pages above (p. 131), the "gnathos absent" statement also appears for *Atarnes hierax*, but not for its congener *A. sallei* (C. Felder & R. Felder, 1867). *A. hierax* is characterized by: "arms of uncus very long and slender." The genitalic sketches for *A. hierax* and *P. unifasciata* (plate 42, E.45.2 and E.49.1) look very similar to each other and very different from those of their congeners (e.g. E.45.1. and E.49.2 for comparison); being similar to the extent that allowing for imprecision in drawing, they may be taken to depict the same species. Did Evans mix up the genitalia and illustrate the same species under different names?

A combination of evidence from genitalia,

Received: 19 September 2012

Accepted: 13 November 2012

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morphology of immature stages, and COI mtDNA sequences strongly argues that *P. unifasciata* and *A. hierax* have been misclassified and attributed to genera they do not belong in. Moreover, despite a highly distinct superficial appearance, they are likely to be each others' closest known relatives. For these reasons, a new genus *Eburuncus* is erected for them.

## MATERIALS AND METHODS

Specimens used in this study were from the following collections: National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM); Museum für Naturkunde, Berlin, Germany (ZMHB); Natural History Museum, London, UK (BMNH); and Texas A&M University Insect Collection, College Station, TX, USA (TAMU). Standard entomological techniques were used for dissection (Robbins, 1991), i.e. the adult abdomen being soaked for 24 hours in 10% KOH at room temperature, dissected and subsequently stored in a small glycerol vial pinned under the specimen. Genitalia and wing venation terminology follow Klots (1970) and Comstock (1918), respectively. Most photographs were taken using a Nikon D200 camera; for specimens through a 105mm f/2.8G AF-SVR Micro-Nikkor lens, and for genitalia through a transillumination microscope. DNA sequences reported in Janzen *et al.* (2011) were downloaded from GenBank <http://www.genbank.gov/>, aligned by hand since insertions or deletions were absent, and analyzed using the Phylogeny.fr server at <http://www.phylogeny.fr/> with default parameters (Dereeper *et al.* 2008).

## History of *P. unifasciata* and *A. hierax* taxonomy

*Leucochitonea unifasciata* C. Felder & R. Felder, 1867 was named from "Nova Granada: Bogota", today's Colombia, from an unstated number of male specimens. A syntype is in BMNH (examined, photographed, dorsal side available in Warren *et al.*, 2012). Listed once as *Entheus unifasciata* by Kirby (1871) and *Pythonides unifasciata* by Plötz (1884), it was finally and stably placed in the newly described genus *Potamanax* (Watson, 1893; type species *Leucochitonea flavofasciata* Hewitson, 1870). Since this genus name was already occupied by Pilsbry, [1893] (in Mollusca) for about 4 months at the time of description, *Potamanax* was suggested by Lindsey (1925) to replace Watson's junior homonym. With the odd exception of Lewis (1973) and Moreno *et al.* (1998) who placed it in *Carrhenes* Godman & Salvin, 1895, *unifasciata* has always been listed in *Potamanax*/*Potamanaxas* or its various misspellings since Watson (1893; Mielke, 2005).

*Milanion marica* Godman & Salvin, 1895 was named from Nicaragua: Chontales in the newly described genus *Milanion* (type species *Papilio hemes* Cramer, 1777). The holotype (by monotypy) is in BMNH (examined, photographed, dorsal side available in Warren *et al.*, 2012). Godman and Salvin (1895) expressed some doubt about the generic assignment of *marica*, writing: "It bears some resemblance to *Potomanax*." Evans (1953) synonymized *marica* with *P. unifasciata*, which does not conflict with the evidence available to me.

*Pythonides hierax* Hopffer, 1874 was named from Peru: Chanchamayo. A series of 2 likely and 2 possible syntypes is in ZMHB (examined, photographed, available in Warren *et al.*, 2012). Plötz (1884) named this species *P. servatius*, a name which is therefore an objective junior synonym. Mabilie (1903) transferred it (as *servatius*) to the genus *Atarnes* Godman & Salvin, 1897 (type, and only included species *Leucochitonea salléi* C. Felder & R. Felder, 1867), where it has resided since.

## RESULTS

### Generic placement of *P. unifasciata* and *A. hierax*

**Adults:** As stated above, *unifasciata* should not be included into *Potamanaxas*. All *Potamanaxas* species possess in their male genitalia a gnathos, uncus arms that are shorter than or equal to the tegumen in length (Figs. 4gk), and brush organs at the bases of valvae. In addition, they are all characterized by the absence of secondary sexual characters in males and the absence of forewing subapical hyaline spots (Evans, 1953) (Figs. 1ij, 2ef). "*P.*" *unifasciata* lacks a gnathos and its uncus arms are at least 1.5 times longer than the tegumen (Figs. 4ab); its males possess several notable secondary sexual characters, such as a thoracic pouch, hair tuft on the hind tibia (Fig. 3a) and a vestigial costal fold; and the forewing of both sexes has distinct subapical hyaline spots (usually all 5 of them are developed; Figs. 1ab, 2ab). These differences were noted in Evans (1953), who contrasted *unifasciata* with all the rest of *Potamanaxas* species in his key. In addition, the light discal bands on the forewing of *Potamanaxas* do not show hyalinity (Figs. 1ij, 2ef). In contrast, *unifasciata* (Figs. 1ab, 2ab), like *Milanion* spp. (Figs. 1ef, 2c) and some other Achlyodini Burmeister, 1878 (Figs. 1cdgh, 2d), possesses hyaline areas in the discal band. The main similarity between *unifasciata* and some *Potamanaxas* species is the general look of the wing patterns: dark wings with white discal bands (Figs. 1abij, 2abef).

**Larvae:** Analysis of photographs of immature stages



corroborates that *unifasciata* is not a *Potamanaxas* (Fig. 5). As with many other Erynnini Brues & Melander, 1932 (photographs in on-line databases by Janzen & Hallwachs, 2012 and Warren *et al.*, 2012), later instar caterpillars of *Potamanaxas* (Fig. 5f) and the closely related *Mylon* Godman & Salvin, 1894 (Fig. 5g) possess a heart-shaped, trapezoid or almost triangular head, which widens dorsally as seen in anterior view. In photographed caterpillars representative of other Pyrginae Burmeister, 1878 tribes, especially in Achlyodini (apparently misspelled as Achlyodidini in Warren *et al.*, 2008; 2009), the head is more rounded, and is not significantly swollen dorsally in most cases (Figs. 5cd; Janzen & Hallwachs, 2012; Warren *et al.*, 2012). Although I could not find a photograph of a *unifasciata* caterpillar, an image of a pupa with larval skin still attached clearly shows a rounded head (Fig. 5a), very similar to that observed in *Milanion marci* Godman & Salvin, 1895 (Fig. 5c). In addition, caterpillars of *unifasciata*, *M. marci* and *Atarnes sallei* all use Annonaceae as foodplants, while three *Potamanaxas* species reared from Guanacaste (NW Costa Rica) utilize Ericaceae (Janzen & Hallwachs, 2012). The immature stages of *A. hierax* have not been recorded.

**Pupae:** Pupal characters are even more revealing. Out of 18 genera placed in Erynnini by Warren *et al.* (2008; 2009), photographs of pupae are available for at least one species from 11 genera (Janzen & Hallwachs 2012; Warren *et al.*, 2012). All of these Erynnini taxa are characterized by a broad and stout pupa with short abdomen and a prominently developed pair of black spiracles on the thorax ('counterfeit eyes' per Janzen *et al.*, 2010). Erynnini pupae are almost always green, shiny and without bloom (Fig. 5h); however, after diapause, discolored caterpillars may produce whitish and brownish pupae as the one shown for *Erynnis persius fredericki* H. Freeman, 1943 (Fig. 5i). The pupal head capsule is rounded between the eyes. Certain genera of smaller Achlyodini skippers have more gracile, slender pupae with longer abdomens and smaller thoracic spiracles concolorous with the rest of the body, which is mostly whitish, yellowish or brown, sometimes covered in white bloom (Fig. 5e; Janzen & Hallwachs, 2012; Warren *et al.*, 2012). These Achlyodini display an anterior protuberance of the head capsule, sometimes consisting of a sharp horn-like point, with prominent concave surfaces formed between it and the eyes (pointed to by an arrow on Fig. 5e). The "*P.*" *unifasciata* pupa (Fig. 5a) possesses these Achlyodini characters as listed above, rather than Erynnini characters.

**DNA barcodes:** The 654-nucleotide mitochondrial DNA sequence of the C-terminal region of the

cytochrome c oxidase subunit 1 (COI) gene, dubbed "barcode", offers further support for the placement of *unifasciata* among Achlyodini instead of in *Potamanaxas*, and not even among Erynnini. Six taxa with barcode sequences reported by Janzen *et al.* (2011) were chosen for analysis (Fig. 6). "*P.*" *unifasciata* and *P. cf. hirta*, which is somewhat similar to *unifasciata* in wing pattern, represent Evans' *Potamanaxas*. *P. cf. hirta* called "*Potamanaxas* Burns01" (Janzen & Hallwachs, 2012) is an undescribed species somewhat similar to *P. hirta* (Weeks, 1901), and it has its DNA barcode sequence available (Janzen *et al.*, 2011). *Mylon lassia* (Hewitson, 1868) was used to represent a sister genus to *Potamanaxas*. *M. marci* and *A. sallei* are representatives of Achlyodini with similar immature characteristics to "*P.*" *unifasciata*. Finally, *Drephalys alcmon* (Cramer, 1780) is from a different subfamily (Eudaminae Mabille, 1877) than the other taxa (Pyrginae Burmeister, 1878) and was used as outgroup to root the tree. Although barcode sequences are typically too short for confident phylogenetic inference, sometimes statistically supported and consistent results can be obtained. For instance, all four different phylogenetic methods offered at Phylogeny.fr web server (BioNJ, PhyML, MrBayes and TNT; Dereeper *et al.*, 2008) produced trees identical in topology, and statistical support for all internal nodes was close to 1. The trees according to the first and the last method mentioned above are shown in Fig. 6. One would expect the two *Potamanaxas* species to be sisters. However, that was not the case. *Mylon* and *P. cf. hirta* came out as sister taxa, but *unifasciata* grouped with *Milanion* and *Atarnes* on the other side from the root. Careful inspection of the multiple sequence alignment revealed the reasons (Fig. 6). At least 30 positions (red, magenta and green) voted against sister relationship between the two *Potamanaxas* species by supporting their grouping with other taxa, and only one position (blue) supported it. Furthermore, an analysis of evolutionary distances between sequences in terms of numbers (or %) of different nucleotides leads to the same conclusion. Distances were smallest between *unifasciata* and *Milanion* (6.4%) on the one hand, and between *P. cf. hirta* and *Mylon* (8.9%) on the other, suggesting these pairings of taxa to be sisters within the taxon sample under study. 6.4% is a very close distance indicative of tribal, and possibly even congeneric, relationship. Thus, DNA analysis aligns "*P.*" *unifasciata* with *Milanion*, which agrees with Godman & Salvin's (1895) placement of its synonym *marica* in *Milanion*, and is inconsistent with a *Potamanaxas* that includes *unifasciata* being monophyletic. In summary, all lines of evidence, from







morphological to molecular, argue that *unifasciata* is not a *Potamanaxas*. DNA sequences of *A. hierax* have not been reported.

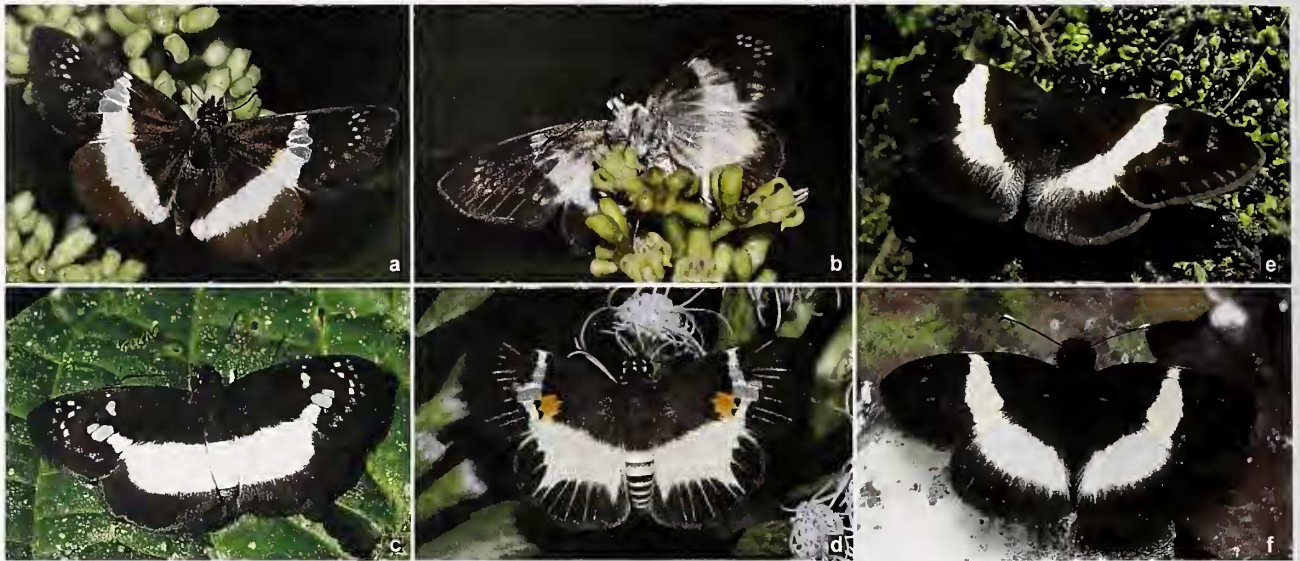
**Finding a new genus for *unifasciata*:** Among the genera *unifasciata* has been formerly placed in, none is suitable. The type species *levubu* Wallengren, 1857 of the original genus *Leucochitonea* belongs to Tagiadini Mabilie, 1878, an exclusively Old World tribe (Warren, 2009), characterized by anal wool in females (Evans, 1937; Warren *et al.*, 2009). In addition, all three (exclusively African) species currently in *Leucochitonea* have a very short uncus (Evans, 1937). *Entheus* Hübner, [1819] is in a different subfamily (Eudaminae) and is characterized by very different palpi with the third segment being stout and spatulate, positioned close to the outer edge of the second segment (Evans, 1952). *Pythonides* Hübner, [1819] also differs in palpi: the 3rd segment is shorter than the 2nd, and in addition its uncus is undivided (Evans, 1953). *Carrhenes* Godman & Salvin, 1895 is characterized by a short uncus, developed gnathos, rounded wings with variegated pattern and a strongly developed costal fold in males. Finally, DNA barcodes are available for representatives of all these genera (except *Leucochitonea*), and they do not root close to *unifasciata* (data not shown).

Interestingly, when Evans' (1953) key for genera in group "E" is used to identify *unifasciata* and 49a (p. 15; "H costa and dorsum sub-equal") is correctly chosen over 40b (p. 13; "H longer at costa than at dorsum"), it keys to *Carrhenes* ("F vein 12 long, ending over end cell") instead of *Potamanaxas* ("F vein short and vein 11 ends over end cell"), except that the costal fold in males is vestigial. However, if 40b is selected over 49a, then it keys to the choice between *Atarnes* (broad white forewing band, orange spot on the forewing) and *Milanion* (hyaline forewing spots, "no red or

yellow spots"). Many specimens of *unifasciata* exhibit a narrow area of orange scales along the basal edge of the forewing white discal band, more prominent in the posterior half (Figs. 1b, 2a). This area does not quite qualify as the "spot" of *Atarnes*, but in combination with the white forewing band it suggests the choice of *Atarnes* over *Milanion* in the Evans key. However, placing *unifasciata* in *Atarnes* causes problems with monophyly of this latter genus in DNA barcode data, since *unifasciata* is sister to *Milanion* and only their common ancestor is sister to *Atarnes sallei* (Fig. 6), a strongly supported hypothesis. Alternatively, it seems plausible to place *unifasciata* in *Milanion* instead, and simply change the Evans key.

However, further look into *Atarnes* reveals a more compelling option. Indeed, the two species in *Atarnes*, *sallei* and *hierax*, have very different genitalia (Fig. 4), as noted in Evans (1953). The *A. sallei* uncus is much shorter, the gnathos is present, its valva lacks a style, and the harpe is quite extended without a prominent tooth dorsad (Figs. 4hl). The *A. hierax* uncus is very long, about twice as long as the tegumen, the gnathos is absent, and the valva has a prominent style and a large tooth on a shorter harpe (Figs. 4cdei). Although both species possess a thoracic pouch (Figs. 3bc), it is somewhat different in shape, being wider in *A. sallei* (Fig. 3c). The *A. hierax* pouch is more slender (Fig. 3b), and similar to that of "*P.* *unifasciata* (Fig. 3a). Even wing patterns, despite superficial resemblance, reveal curious differences. In *A. hierax*, white streaks are along the veins (Figs. 1cd), but in *A. sallei* they are mostly between the veins in the middle of each cell (Figs. 1gh). Moreover, the position of the orange forewing spot differs. In *A. hierax* this spot is bordering the basal boundary of the white discal band and is more diffuse and absent ventrally, but in *A. sallei* it is inside the brown basal area, is more defined, is

**Figure 1 (Opposite page). Spread adults.** The letter is placed between the images of the same specimen. Dorsal above or left, ventral below or right. 1cm scale is shown for each specimen between the two images. "F" indicates that a mirror image (i.e. left-right inverted) is shown. Unless indicated otherwise (c, d, g.), specimens are from Costa Rica, Area de Conservacion Guanacaste and are in USNM collection. a, b. *Eburuncus unifasciata*, a. ♂ Guanacaste Prov., Guacimos, 380m, collected on 21-VI-2006, eclosed on 07-VII-2006, foodplant *Annona rensoniana* (Annonaceae), voucher code 06-SRNP-21553; b. ♀ Guanacaste Prov., Sector Cacao, Sendero Arenales, 1080m, collected on 15-VIII-1994, eclosed on 19-VIII-1994, foodplant *Annona rensoniana* (Annonaceae), voucher code 94-SRNP-6414; c, d. *Eburuncus hierax*, c. likely syntype ♂ Peru: Chanchamayo, leg. Thamm, [ZMHB]; d. ♂ Peru, from Geo G. MacBean, genitalia NVG120922-36 [USNM], (genitalia on Fig. 4de, thoracic pouch on Fig. 3b); e, f. *Milanion marciana*, e. ♂ Alajuela Prov., Sector Rincon Rain Forest, Camino Rio Francia, 410m, collected on 28-IX-2004, eclosed on 18-X-2004, foodplant *Annona papilionella* (Annonaceae), voucher code 04-SRNP-42477; f. ♀ Alajuela Prov., Sector San Cristobal, Sendero Huerta, 527m, collected on 02-III-2007, eclosed on 31-III-2007, foodplant *Annona rensoniana* (Annonaceae), voucher code 07-SRNP-1128; g, h. *Atarnes sallei*, g. ♂ Mexico: Tamaulipas, Sierra Cucharas, nr. rock quarry, ex larva, foodplant *Annona globiflora* (Annonaceae), eclosed 28-I-1975, leg. Roy O. Kendall & C. A. Kendall [TAMU]; h. ♀ Guanacaste Prov., Sector Mundo Nuevo, Mamones, 365m, collected on 24-VIII-2006, eclosed on 19-IX-2006, foodplant *Annona rensoniana* (Annonaceae), voucher code 06-SRNP-57921; i, j. *Potamanaxas* cf. *hirta* (Burns01), i. ♂ Guanacaste Prov., Sector Pitilla, Sendero Memos, 740m, collected on 29-III-2007, eclosed on 18-IV-2007, foodplant *Cavendishia axillaris* (Ericaceae), voucher code 07-SRNP-31875; j. ♀ Guanacaste Prov., Sector Pitilla, Sendero Memos, 740m, collected on 16-IV-2011, eclosed on 13-V-2011, foodplant *Cavendishia axillaris* (Ericaceae), voucher code 11-SRNP-31012. Pinholes and some other imperfections have been digitally removed to emphasize all actual elements of the pattern, such as small white spots.



**Figure 2.** Live adults. **a, b.** *Eburuncus unifasciata*, dorsal and ventral views, Mexico: Veracruz, Ruiz Cortines, 5-VI-2008, Bill Bouton; **c.** *Milanion* sp., Panama: Darien, Cana Field Station, 07-I-2003, Will & Gill Carter; **d.** *Atarnes sallei* Mexico: Tamaulipas, Los Troncones Canyon, 18-XI-04, Kim Davis & Mike Stangeland; **e, f.** *Potamanaxas* spp. cf. *hirta* or *thoria*, **e.** Ecuador: Pastaza Province, Palora, Santa Rosa, -1.43° -78.00°, 900m, 19-VIII-2011, Pierre Boyer; **f.** Colombia: Dept. Risaralda, Otun, Quimbaya Reserve above Pereira, 1800m, 13-IX-2010, Kim Garwood. Hyaline areas are visible as darker patches inside the white forewing bands in **a-d**. No hyalinity is seen in **e, f.** *P.* spp.

present on both wing surfaces and is separated from the white discal band by patches of brown scales. Due to these genitalic and wing pattern differences in the two *Atarnes* species, and the profound similarities of *A. hierax* genitalia with those of *P. unifasciata* (Fig. 4ab), it is most likely that the streaky orange-spotted patterns are convergent. “*P.*” *unifasciata* is a likely sister species of *A. hierax*, which would make *Atarnes* polyphyletic. Thus, to be consistent with all available data and to suggest a phylogenetic hypothesis best supported by existing evidence, either *A. hierax* together with *P. unifasciata* should be transferred to *Milanion*, or a new genus should be erected for these two taxa. Since all seven *Milanion* species are quite close to each other in wing patterns and genitalia (Evans, 1953), thus forming a tight cohesive group, and none of them possesses a long uncus, a style on the valva and lacks the gnathos (Fig. 4fj), it appears that a new genus hypothesis should be preferred, and this new genus is named here.

#### ***Eburuncus* Grishin, new genus**

(Figs. 1a-d, 2ab, 3ab, 4a-d,i, 5ab)

**Type species:** *Leucochitonea unifasciata* C. Felder & R. Felder, 1867

**Diagnosis:** Very long and slender uncus arms (more than 1.5x tegumen length) combined with the absence of a gnathos is the defining character and a synapomorphy for the genus (Figs. 4a-d,i). Other possible synapomorphies that are present in all

known species of this genus include the shape of the valva with a rectangular process, the harpe with a prominent single tooth on the dorsal surface, and a forewing pattern consisting of a white discal band partly hyaline distally in discal cell and cell  $CuA_1$ - $CuA_2$ , frequently with areas of orange scales along its basal edge, more developed in the posterior part, and subapical hyaline spots (Figs. 1a-d, 2ab). A combination of these characters differentiates species of this new genus from related or similar taxa. Other characters are detailed in the description.

**Description.** **Forewing** Sc vein long, reaching the end of discal cell, background color brown, subapical hyaline spots, discal white band with hyaline areas in discal cell and cell  $Cu_1$ - $Cu_2$ , frequently with a patch of orange scales along the basal edge, more expressed in the posterior half. **Hindwing** margin brown, base brown dorsally and lighter ventrally, white discal band or patch near costa. **Antenna** about half of costa length, bent from beginning of nudum of 14-16 segments, apiculus about equal in length to the rest of club. **Palpi** porrect with the 3rd, narrower segment in the middle of 2nd segment and as long as the 2nd segment. **Male secondary sex characters:** hind tibiae with a tuft of scales fitting in a thoracic pouch. Costal fold either absent or vestigial. **Male genitalia:** gnathos absent, arms of uncus very long and slender, close to twice the length of tegumen and about half of valval length, saccus short, shorter than the style on the valva. **Variation:** one species with whitened veins, broader forewing discal white band and larger orange spot; the other species with 5 instead of 2 forewing apical hyaline spots, a hyaline spot at the base of  $M_3$ - $CuA_1$  forewing cell and a broad discal band on the hindwing from costa to tornus instead of a white patch not reaching the tornus.

**Species included:** *Leucochitonea unifasciata* C. Felder & R. Felder, 1867 with its junior subjective synonym *Milanion marica* Godman & Salvin, 1895; and *Pythonides hierax* Hopffer, 1874 with its junior objective synonym *P. servatius* Plötz, 1884.

**Etymology:** The name is a composite of two words “ebur” (ivory, ivory objects, and also elephant) and “uncus” (the terminal





**Figure 3. Thoracic pouch and tibial tufts.** a. *Eburuncus unifasciata* Panama: Cerro Campana, 1500', 9-X-1966, leg. G. B. Small, genitalia NVG120207-01 [USNM] (genitalia on Fig. 4ab); b. *Eburuncus hierax*, Peru, from Geo G. MacBean, genitalia NVG120922-36 [USNM], (specimen on Fig. 1d, genitalia on Fig. 4de); c. *Atarnes sallei* Costa Rica: Guanacaste Prov., Area de Conservacion Guanacaste, Sector Mundo Nuevo, Porton Rivas, 570m, collected on 07-VIII-2007 as penultimate instar, eclosed on 26-VIII-2007, foodplant *Annona pruinosa* (Annonaceae), voucher code 07-SRNP-58936, genitalia NVG120922-28 (Fig. 4h) [USNM], mirror image (=left-right inverted).

hook-like structure in the male genitalia). It points to the defining character of the genus: a very long uncus with arms shaped akin to elephant tusks. Although not as provocative as *Cornuphallow* (translation: "hornydick", jokingly coined by George T. Austin), *Eburuncus* (translation: "tuskhook") continues the interesting tradition suggested by G. T. Austin of naming genera by peculiar features of male genitalia. The name is a masculine noun in the nominative singular.

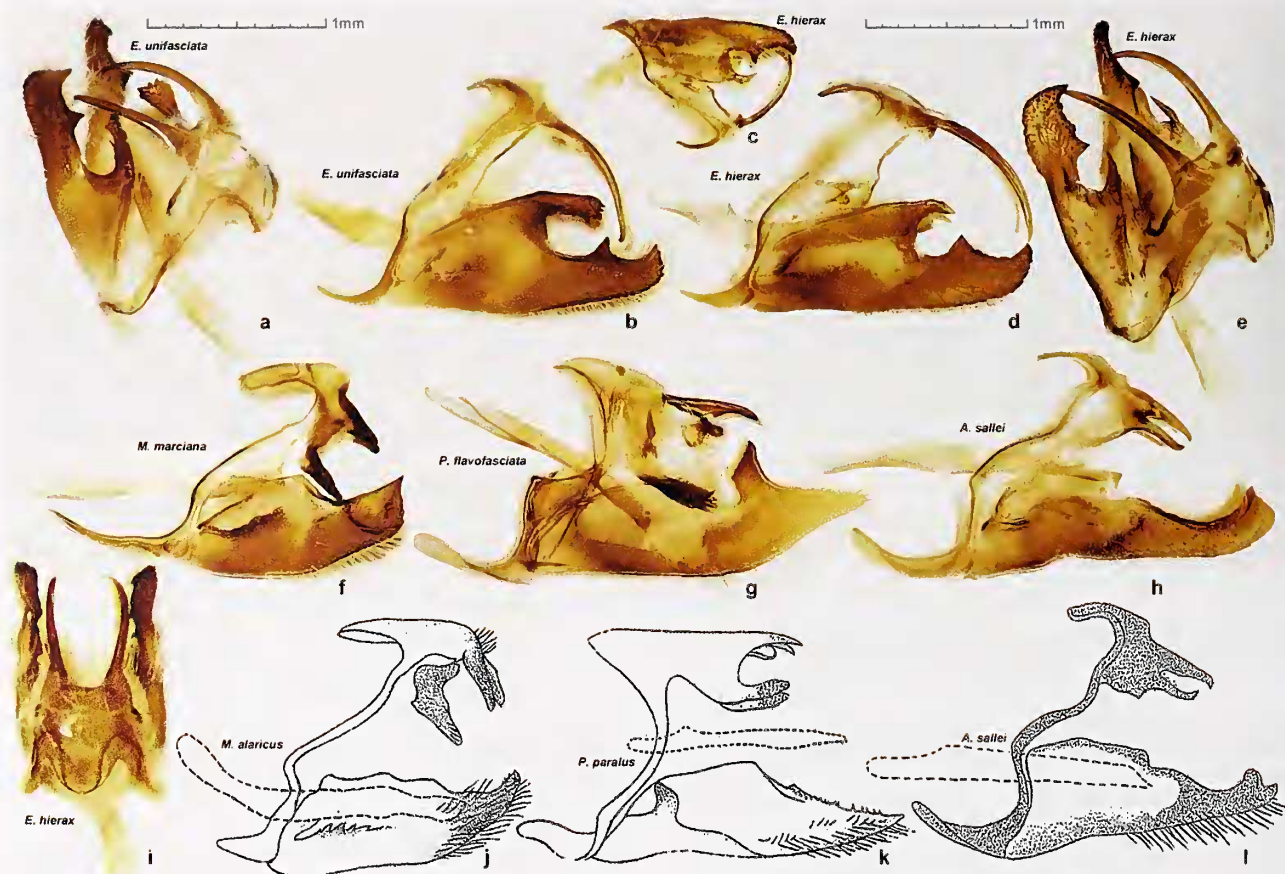
## DISCUSSION

Male genitalia remain the primary guiding bedrock for HesperIIDae classification as they are diverse and rarely undergo convergence. The likely convergent streaky patterns of *A. sallei* and *E. hierax* remind us that to achieve classification better reflecting evolutionary relationships, every hesperiid genus should be scrutinized and male genitalia carefully examined. To detect convergent patterns, close comparison is in order. Superficial streaky appearance is intrinsically different in these two species. *E. hierax* has white veins, but *A. sallei* has white rays developed mostly between the veins in the middle of each cell. The orange spot is a part of the edge between the brown base and white discal band in *E. hierax* (as it is in *E. unifasciata*), but is a semi-square area inside the brown base in *A. sallei*.

While it is not possible to confidently predict what yet undiscovered species, if any, would be placed in this new genus and thus what characters, especially wing patterns, they would possess, the description of *Eburuncus* **gen. nov.** summarizes those characters that are likely to be synapomorphic, including wing

patterns. These characters, in accordance with ICZN Code (1999) Article 13.1.1 and Recommendation 13A, are common to both species in the genus and differentiate them from all other described species. However, for newly discovered species attribution to the genus should be based on phylogenetic considerations rather than a blind application of all the characters listed in the description, as it is possible that some of these characters may not portray some of the species yet to be discovered.

A genus, being a primary taxonomic group between the family and species ranks, should be defined with care. Both over- and undersplitting hinders communication between researchers. When a new genus is proposed, a primary concern should be whether an unnecessary synonym might be created. Standards in defining a genus may vary between taxa and the history of generic usage for a particular group should be taken into account. A new genus should be most consistent with genera traditionally in use for the closest taxa. Current evidence suggests that *Eburuncus* **gen. nov.** and *Milanion* are sisters. Thus, in principle, *E. unifasciata* and *E. hierax* could be treated under *Milanion* to create a larger and more diverse genus. However the hiatus between *Eburuncus* **gen. nov.** and *Milanion*, taking into account the similarity in genitalia within each genus, is quite large. Wing patterns also readily distinguish them. Both *Eburuncus* **gen. nov.** species have a complete white discal band on the forewing starting from the costa and frequently an area of orange scales. In *Milanion*, the band is incomplete and does not reach the costa,



**Figure 4. Male genitalia.** a, b. *Eburuncus unifasciata* Panama: Cerro Campana, 1500', 9-X-1966, leg. G. B. Small, genitalia NVG120207-1 [USNM] (thoracic pouch on Fig. 3a); c, i. *Eburuncus hierax*, likely syntype, Peru: Chanchamayo, leg. Thamm, genitalia NVG120717-3 [ZMHB]; d, e. *Eburuncus hierax*, Peru, from Geo G. MacBean, genitalia NVG120922-36 [USNM], (specimen on Fig. 1d, thoracic pouch on Fig. 3b). f. *Milanion marciiana* Costa Rica: Alajuela Prov., Area de Conservacion Guanacaste, Sector Rincon Rain Forest, Camino Rio Francia, 410m, collected on 28-IX-2004, eclosed on 18-X-2004, foodplant *Annona papilionella* (Annonaceae), voucher code 04-SRNP-42477, genitalia NVG120922-25 [USNM]; g. *Potamanaxas flavofasciata flavofasciata* (Hewitson, 1870), Peru: Amazonas, 4km W Abra Wawajin, 05° 18'S 78° 24'W, 750m, 24-IX-1999, leg. R. K. Robbins & G. Lamas, genitalia NVG120922-32 [USNM]; h. *Atarnes sallei*, Costa Rica: Guanacaste Prov., Area de Conservacion Guanacaste, Sector Mundo Nuevo, Porton Rivas, 570m, collected on 07-VIII-2007 as penpenultimate instar, eclosed on 26-VIII-2007, foodplant *Annona pruinosa* (Annonaceae), voucher code 07-SRNP-58936, genitalia NVG120922-28 [USNM] (thoracic pouch on Fig. 3c); j. *Milanion alaricus* (Plötz, 1884), pl. 87, f. 1, identified by Evans (1953), not *M. hemes* or *M. leucaspis* (Mabille, 1878) as in the Godman & Salvin (1895) plate caption or text; k. *Potamanaxas paralus* (Godman & Salvin, 1895), original illustration of a syntype genitalia, Peru: Cosnipata Valley, leg. H. Whitely, pl. 86, f. 1; l. *Atarnes sallei*, pl. 90, f. 16. Drawings e. and f. are from Godman & Salvin (1895) and g. is from Godman & Salvin (1897). Scale on the left refers to a, b, f, g, h. Scale on the right refers to d and e. Other images are not to scale.

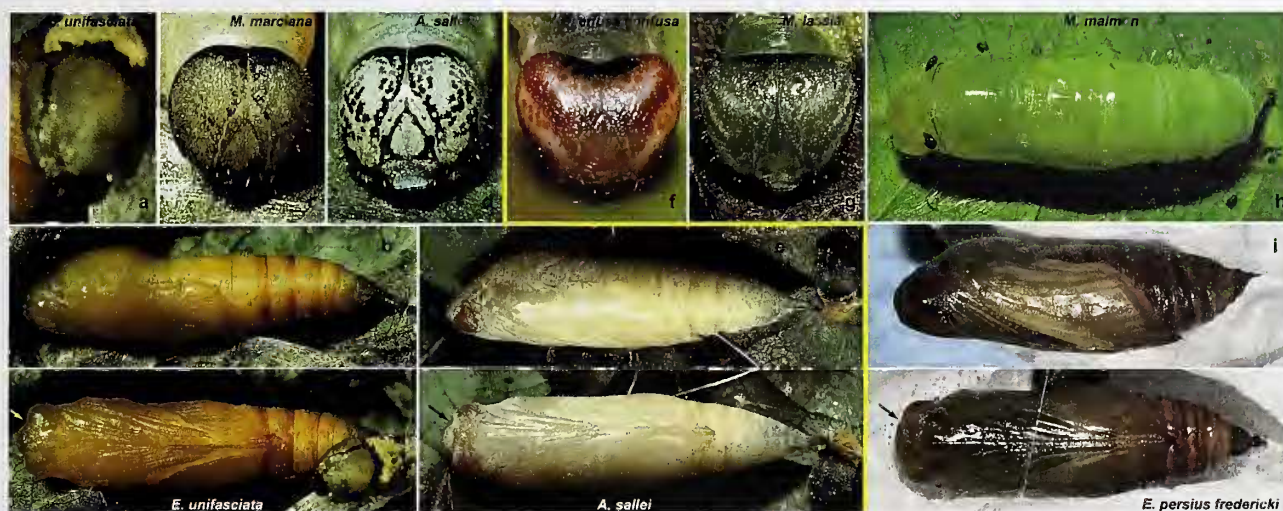
and no orange scales are observed. Additionally, we see a trend in the recent literature to propose a finer generic structure for HesperIIDae, with smaller and more cohesive, frequently monotypic genera (Steinhauser, 1989; Austin & Warren, 2001; Austin, 1997; 2008). Therefore erection of *Eburuncus* gen. nov. is both biologically and historically justifiable.

Barcode sequences of mtDNA COI, although they are too short for confident phylogenetic inference, have been very helpful for the analysis of HesperIIDae diversity (Janzen *et al.*, 2011) and could be an excellent

source of phylogenetic hypotheses requiring further corroboration. Conversely, barcodes could be used as additional evidence along with morphological characters to support hypotheses suggested on the basis of other data. However, even in HesperIIDae, where the COI barcode typically correlates well with divergence of species, due to frequent cases of introgression (Zakharov *et al.*, 2009) it is not advisable to base phylogenetic conclusions entirely on a small sample of barcodes.

A COI DNA barcode distance of 6.4% agrees





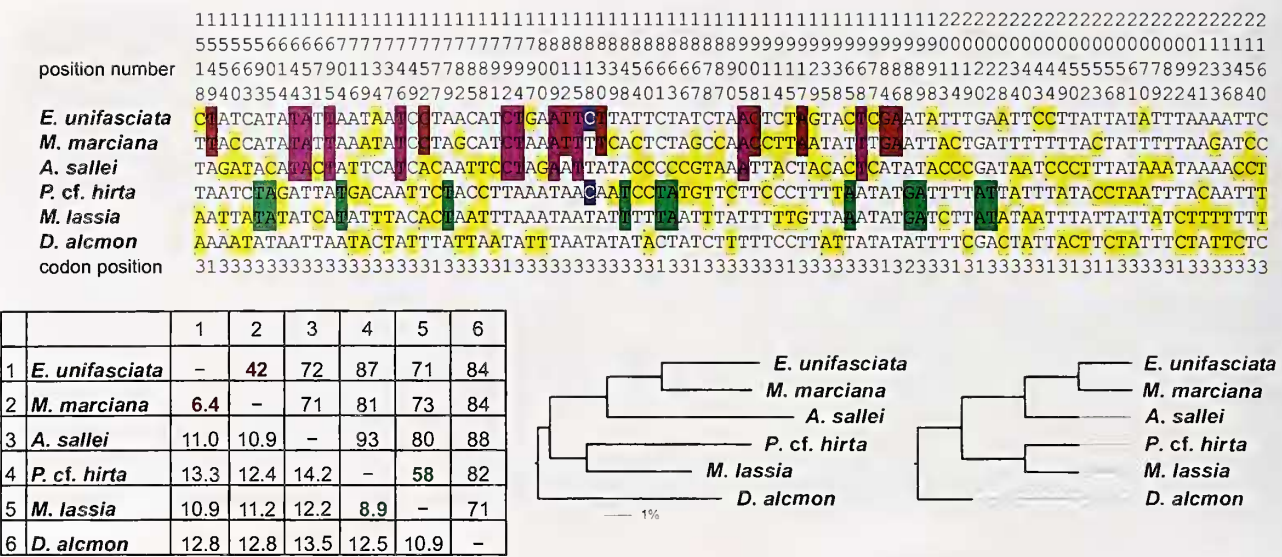
**Figure 5. Immature stages.** All specimens are from Costa Rica, Area de Conservacion Guanacaste except i., which is from USA: Utah. **a, b.** *Eburuncus unifasciata*, Guanacaste Prov., Sector Cacao, Sendero Arenales, 1080m, collected on 10-II-1995, photographed on 25-II-1995, foodplant *Annona rensoniana* (Annonaceae), voucher code 95-SRNP-438, image codes DHJ21801 (a. and b. below) and DHJ21797 (b. above); **c.** *Milanion marciana*, Alajuela Prov., Sector Rincon Rain Forest, Camino Rio Francia, 410m, collected on 26-VI-2002, photographed on 09-VII-2002, foodplant *Annona papilionella* (Annonaceae), voucher code 02-SRNP-7566, image code DHJ67669; **d, e.** *Atarnes sallei*, Guanacaste Prov., d. Sector Cacao, Sendero Maritza, 760m, collected on 19-II-1997, photographed on 16-III-1997, foodplant *Annona rensoniana* (Annonaceae), voucher code 97-SRNP-678, image code DHJ40302; **e.** Sector Santa Rosa, Las Mesas, 305m, collected on 09-XII-1992, photographed on 02-I-1993, foodplant *Annona purpurea* (Annonaceae), voucher code 92-SRNP-6105, image codes DHJ16973 (above) and DHJ16970 (below); **f.** *Potamanaxas effusa confusa* (Draudt, 1922), Alajuela Prov., Sector Brasilia, Piedrona, 340m, collected on 07-XI-2007, photographed on 19-XI-2007, foodplant *Satyria panurensis* (Ericaceae), voucher code 07-SRNP-65901, image code DHJ435325; **g.** *Mylon lassia*, Guanacaste Prov., Sector Del Oro, Quebrada Romero, 490m, collected on 21-VIII-2002, photographed on 07-IX-2002, foodplant *Cissampelos pareira* (Menispermaceae), voucher code 02-SRNP-28838, image code DHJ70894; **h.** *Mylon maimon* (Fabricius, 1775), Guanacaste Prov., Sector Santa Rosa, Vado Cuajiniquil, 5m, collected on 18-X-1993, photographed on 03-XI-1993, foodplant *Heteropterys laurifolia* (Malpighiaceae), voucher code 93-SRNP-6934, image code DHJ26415; **i.** *Erynnis persius fredericki* H. Freeman, 1943 USA: Utah: Davis Co., Francis Peak, 12-(above) & 5-(below)-III-2007. **a, c, d, f, g.** Larval heads in anterior view, **a.** is a head capsule with skin still attached to pupa. **b, e, h, i.** Pupae. Except for **h.** (*M. maimon*) shown in dorsal view, others are shown in lateral and ventral views above and below, respectively; **e.** shows a mirror image (i.e. left-right inverted). Arrow points at an area between eye and anterior portion of the head capsule, which is concave in small Achlyodini skippers and mostly flat in Erynnini. All images are from the Janzen & Hallwachs database (2012) <http://janzen.sas.upenn.edu/caterpillars/database.lasso>, except **i.**, which is by Nicky Davis.

well with the distances observed between species from very close genera in Eudaminae and Pyrginae (Janzen *et al.*, 2011). For instance, one of the smallest intergeneric distances is found between *Achalarus* and *Thessia* – only 3.5% between *A. toxus* (Plötz, 1882) and *T. jalapus* (Plötz, 1881). Comparable distances to *Eburuncus*-*Milanion* are seen between *Heliopetes* Billberg, 1820 and *Heliopyrgus* Herrera, 1957: 4.9% [*H. ericetorum* (Boisduval, 1852) and *H. domicella* (Erichson, [1849])]; *Pseudonascus* Austin, 2008 and *Nascus* Watson, 1896: 7.3% [*P. paullinae* (Sepp, [1842]) and *N. solon* (Plötz, 1882)]; *Eantis* Boisduval, 1836 and *Achlyodes* Hübner, [1819]: 8.4% [*E. tamenund* (W. H. Edwards, 1871) and *A. pallida* (R. Felder, 1869)]; and *Salatis* Evans, 1952 and *Nicephellus* Austin, 2008: 8.9% [*S. canalis* (Skinner, 1920) and *N. nicephorus* (Hewitson, 1876)]. These distances are given here for

the purpose of comparison only, and application of a uniform COI % difference cutoff carries little value in defining a meaningful genus. For instance, the intrageneric distances between some species might be larger than some intergeneric distances, e.g. taking *Achlyodes* and *Eantis*, the distance between *A. pallida* and *A. busirus heros* Ehrmann, 1909 is about 9.5%, which exceeds the distance of 8.4% between *A. pallida* and *E. tamenund*. Each case needs to be analyzed individually and multiple factors considered, such as phylogenetic tree structure, internal branch lengths and statistical significance of nodes.

The example of *E. unifasciata* is quite similar to the example of *Heliopyrgus americanus* (Blanchard, 1852), which in dorsal wing pattern closely resembles *Pyrgus* Hübner, [1819] and was placed in it before genitalic similarities with *H. domicella* and *H. sublinea*





**Figure 6. DNA-derived data.** Multiple sequence alignment (top), distance matrix (bottom left), distance (bottom middle) and maximum parsimony (bottom right) trees are shown. Specimen voucher codes, Genbank accessions and NCBI GI numbers for each sequence are: *Eburuncus unifasciata*: 04-SRNP-364, DQ293104, 84099191; *Milanion marciana*: 04-SRNP-41660, DQ292619, 84098221; *Atarnes sallei*: 06-SRNP-59199, JF760397, 332377953; *Potamanaxas cf. hirta*: 11-SRNP-31012, JQ526704, 374915892; *Mylon lassia*: 04-SRNP-47729, GU161659, 290548094; *Drephalys alcmon*: 00-SRNP-2692, JF752622, 333946838, respectively. *P. cf. hirta* (called “*Potamanaxas Burns01*”) is a likely undescribed species with similarities to *P. hirta*. The aligned 654 positions of COI nucleotide sequences from 6 Hesperidae species correspond to positions 1516-2169 in the *Drosophila yakuba* (Burla, 1954) mitochondrial genome, which is used as the numbering standard, because mitochondrial genomes have different lengths in different taxa. For brevity, only phylogenetically informative positions are shown in the alignment, i.e. invariant positions and positions with a nucleotide difference in a single sequence were removed. *D. yakuba* position numbers are shown above the alignment as columns (e.g., the first shown position is #1518). For each position, its place in a codon (1st, 2nd, or 3rd) is shown below the alignment (“codon position”). Majority of nucleotide changes in the 3rd position (marked as “3”) do not cause a change in a protein encoded by the DNA, thus such changes are more common and are usually subject to more homoplasies. Nucleotides common to *E. unifasciata* and *M. marciana* in positions with nucleotides different from them in all other sequences are highlighted red. These 8 positions most strongly support grouping of these two taxa in a tree. Nucleotides common also to *A. sallei* in addition to the above 2 species, but different from the rest in these positions are highlighted magenta. These 10 positions support grouping of these three taxa in a tree. Nucleotides common to *P. cf. hirta* and *M. lassia* in positions with nucleotides different from them in all other sequences are highlighted green. These 12 positions suggest a sister relationship between these two taxa. There is only a single position that supports *E. unifasciata* being sister to *P. cf. hirta*, (nucleotides in these taxa shown in white on blue), vs. 30 positions strongly supporting alternative trees. All other nucleotides except the most frequent one at each position are highlighted yellow. In the distance matrix, number of nucleotide differences and % of nucleotide differences between sequences are shown above and below diagonal, respectively. For BioNJ distance tree, scale bar corresponds to about 1% difference and all nodes received bootstrap support above 0.9. In TNT parsimony tree branches are not scaled. Topologies of the trees are identical to each other and are in agreement with red, magenta and green highlights in the alignment.

(Schaus, 1902) were brought to light (Herrera *et al.*, 1957; Austin & Warren, 2001). As a result of these studies, *H. domicella* and *H. sublinea* were extracted from the genus *Heliopetes* and united with *P. americanus* under the genus *Heliopyrgus*. However, the remaining *Heliopetes* are quite diverse, so the possibility remains that the genus became paraphyletic as a result. It is not likely that *Milanion* is paraphyletic after exclusion of *Eburuncus* **gen. nov.**, because all seven *Milanion* species are very similar to each other. The forewing lacking orange or red patches but with the white discal band broken into many spots may be synapomorphies for *Milanion* in comparison to the closely related genera

*Eburuncus* **gen. nov.**, *Atarnes*, *Paramimus* Hübner, [1819], *Charidia* Mabilie, 1903, and *Haemactis* Mabilie, 1903 – all of which, at least in females, have orange or red patches on the forewing, and either an entire discal band or zero to two white spots, instead.

**ACKNOWLEDGEMENTS**

I am grateful to Robert K. Robbins, John M. Burns and Brian Harris (National Museum of Natural History, Smithsonian Institution, Washington DC), Wolfram Mey (Museum für Naturkunde, Berlin, Germany), David Lees and Blanca Huertas (Natural History Museum, London, UK), for granting access to the collections under their care and stimulating discussions;



Daniel H. Janzen and Winnie Hallwachs for the photographs of immature stages; Bill Bouton, Nicky Davis, Jean-Claude Petit, Pierre Boyer, Kim Garwood, Will and Gill Carter, Kim Davis and Mike Stangeland for the photographs of live individuals; Bernard Hermier for many enlightening discussions, numerous suggestions, and a most thorough and helpful review of the manuscript; Jonathan P. Pelham for insightful discussion of taxonomic issues and literature; Brian Banker for critical reading of the manuscript and corrections; JRL editor Konrad Fiedler and an anonymous reviewer for helpful comments, modifications and edits. The work to obtain photographs and specimens from ACG has been supported by U.S. National Science Foundation grants BSR 9024770 and DEB 9306296, 9400829, 9705072, 0072730, 0515699, and grants from the Wege Foundation, International Conservation Fund of Canada, Jessie B. Cox Charitable Trust, Blue Moon Fund, Guanacaste Dry Forest Conservation Fund, Area de Conservación Guanacaste, and University of Pennsylvania to Daniel H. Janzen.

## EDITOR'S NOTE

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